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Competitive abilities of oystercatchers (*Haematopus ostralegus*) occupying territories of different quality

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Abstract In territorial species, habitat heterogeneity results in some individuals occupying poor quality sites while others occupy high quality sites. Floaters (mature nonbreeders) may accept a low quality territory, because it is the best they can get and defend ('inferior phenotype hypothesis'), or because it is a strategic alternative for a high quality territory in the long run ('queue hypothesis'). Oystercatcher *Haematopus ostralegus* territories differ consistently in the amount of offspring produced each year and this is related to the distance between the nesting and feeding territories. The inferior phenotype hypothesis was previously rejected on the basis of the absence of morphometric differences (assumed to indicate competitive abilities) among breeders. We investigated social dominance, in the field and in captivity, in relation to the quality of the breeding territory. In the field, birds with high-quality territories won more often compared to those occupying low-quality territories. However, this difference was not apparent in a small dataset of captive birds. These results are discussed in the framework of the long-term fitness prospects of settling in a high or low quality territory.

Keywords Habitat quality · Life history · Phenotypic quality · Settlement

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Introduction

Resources important for survival and reproduction are never divided equally among individuals. The successful acquisition of resources is sometimes correlated with characteristics or traits of the individual. In birds, these traits may cover characteristics of the song (Gil and Gahr 2002), body size dimensions (Verhulst et al. 1997; Larsson et al. 1998; Barbraud et al. 1999) or plumage characteristics (Fugle et al. 1984; Rohwer 1985). In many territorial species, breeding sites are key resources that can vary considerably in quality. Birds that are migratory, or at least part of the year present in another area than the regular breeding area, have to re-occupy a territory each year. Early arriving birds usually occupy the best territories first, excluding the late arriving birds (see Forstmeier 2002 and references therein). This gives rise to a correlation between individual quality (arrival date) and territory quality.

In oystercatchers *Haematopus ostralegus*, the main determinant of annual reproductive success is the quality of the territory, and we can distinguish high and low quality territories at our study site (see Methods). The breeding grounds are saturated with pairs and their numbers were remarkably stable over the years (Heg et al. 2000). Floaters (mature non-breeders) outnumber the number of vacancies and removal experiments showed that settlement is constrained by a shortage of vacancies (Heg et al. 2000; Bruinzeel and van de Pol 2004). Floaters have to be familiar with a small area to successfully obtain a vacancy at that site (Bruinzeel and van de Pol 2004) and density dependent effects cause queuing for high quality territories. The queue hypothesis (Ens et al. 1995) postulates that low and high quality territories might have equal fitness pay-offs, since the benefits of breeding in a high quality territory were presumed to be counterbalanced by a later onset of breeding at these preferred sites. Since the study by Ens et al. (1995) this queuing phenomenon has been regarded as the most likely hypothesis explaining why oystercatchers may accept low quality territories. However, the main alternative, the inferior phenotype hypothesis, also proposed by Ens et al. 1995), has never been tested properly. This hypothesis states that some birds accept poor quality territories because they are poor quality birds. They are not capable of (or despotically excluded from) obtaining a high quality site and as a consequence a low quality territory is the next best they can achieve. This hypothesis was rejected on the basis of a lack of morphometric size differences between owners of various territories. At that time, Ens et al. (1995) admitted that more sophisticated methods of measuring competitive abilities were needed, since the rejection of this hypothesis relied on the assumption that body dimensions were correlated with fighting capacities. Correlations between body dimensions and competitive abilities are not unequivocal in the literature (see Discussion). In this study, we tested competitive abilities of occupants in high- and low-quality sites in a standardised laboratory setting as well as in the field.

Methods

Study site and oystercatcher biology

A population of oystercatchers has been studied for over 20 years on the Dutch island of Schiermonnikoog (53°29′N, 6°14′E). Two types of breeders can be distinguished: residents and leapfrogs. Residents occupy high quality territories and leapfrogs occupy low quality territories (Ens et al. 1992). Residents produce annually 3 times more fledglings compared to leapfrogs because resident territories comprise a nesting territory on the edge of the saltmarsh and an adjacent feeding territory on the mudflats. Leapfrog territories comprise a defended nesting territory located further inland and, usually, a defended feeding area located further offshore. Hence, leapfrogs defend two spatially segregated territories. Chicks are semi-precocial and chicks of residents follow their parents onto the mudflats for food, while chicks of leapfrogs have to wait in the nesting territory for aerial food provisioning (Ens et al. 1992). First row leapfrogs occupy territories adjacent to residents and inland leapfrogs occupy territories further inland (surrounded by other leapfrog territories). In normal years, first row leapfrogs have an average chance of 5% of promoting to resident status, but a slightly larger chance in years following severe winter mortality. Inland leapfrogs do not promote to resident status in normal years (Heg 1999).

Removal of breeding birds (under licence) took place in the breeding season of 1999. The removal was part of an experiment to study the re-occupation process of the created vacancies (Bruinzeel and van de Pol 2004). Given the invasive nature of this experiment, the sample size was necessarily small. Only one individual per breeding pair was removed and all created vacancies were re-occupied within the same or the next season. The birds were caught on the nest and transported to the University of Groningen and housed in cages measuring 2×4×2 m. Three birds of identical sex were caught on 1 day, originating from the three different territory types (resident, first row leapfrog and inland-leapfrog). The next set comprised birds of the other sex and was removed on average 7 days later. All birds caught on the same day were housed in one cage. In total, six males and six females were kept in captivity. The birds were fed ad libitum with trout food pellets and were given twice a day a small amount of thawed cockles *Cerastoderma edule*, their natural food source. Unfortunately, two birds (both females from one cage) died before the dominance measurements took place.

Laboratory experiments

All tests were performed in a cage, which was new for all the birds, approximately 2 weeks after the birds were caught. Prior to the test, we starved the birds for 4 h. During the test period (which lasted 1 h), the birds had access to a tray with fresh water and a tray with food measuring 0.8×0.6×0.1 m filled with mud and 50 hidden cockles. The cockles were hidden just below the surface and were arranged regularly in the tray. All cockles were of one age class (between 20 mm and 25 mm in width) to allow an easy quantification of intake. The frozen cockles were thawed before the experiment and rinsed briefly with hot water until the shells had opened. During the test period, there was no trout food available for the birds and we registered all behaviour on video. We recorded for each bird, every minute, the position and behaviour in the cage (e.g. food intake, feeding and social interactions) until the moment that 75% of all cockles had been eaten. A bird's position was defined as 'near' (i.e. less than one bird-length) the water tray or food tray or 'elsewhere' in the cage (i.e. more than one bird-length away from either of the trays). Initially, we performed tests on three animals in one cage. The assignment of the top-dominant animal was based on direct interactions (dyads, i.e. relations between two animals) and the winscore (the number of interactions won divided by the total number of interactions). However, the determination of the dominance relationships among sub-ordinates were sometimes less conclusive, especially when encounters were rare. The dominance relations were based on at least five interactions per dyad. In some cases these criteria were not met, for instance when a subordinate actively avoided a dominant bird. In those cases, we relied on parameters correlated to the number of interactions won. We first determined the dominance relations among the birds originally removed on the same day and housed together, and subsequently tested birds of different cages randomly against each other. All tests involved only birds of the same sex.

Field experiments

Behavioural observations in the field were collected between January and April 2002 by one observer (C.T.) on the tidal mudflats near the breeding grounds. Marked oystercatchers were located on the mudflats and observations were carried out with a telescope (magnification 20–60 times). Observations were collected on group-foraging birds near the tideline. Observation protocols lasted between 370 and 600 s, and data for different protocols were pooled per individual. All interactions of the focal individual were registered, including the outcome (win or lose). Identities of opponents were not registered and most interactions were 'social aggressions' and were not associated with kleptoparasitism.

All data analyses were conducted using SPSS/PC. Descriptive statistics are given as means ± SE. Statistical tests involving percentages were arcsine transformed prior to testing. Interactions collected in the field were analysed with Hierarchical Linear Models with the observed interaction as the first level and individual as second level.

Results

Captivity

To establish dominance hierarchies we ranked captive birds primarily on the winscore and this allowed us to assign dominance ranks to most of the birds (Table 1).

For the four females, 5 out of the 6 dyads (individual dominance relationships) could be established on agonistic behaviour, for the six males, 8 out of 15. The outcome of a dyad was highly repeatable. In total, eight dyads were repeated (excluding the undecided dyads). Five dyads consisted of duplo trials and three dyads consisted of triplet trials. The outcome of all second- and third-trials was identical to the outcome of the first trial. The probability for finding such an effect at random is $P = 0.5^{11}$ and even if we include each individual only once, to exclude all possible pseudo-replication, the remaining four dyads (♀1–2, ♀3–4, ♂1–5, ♂2–3) still show a significant repeatability of $(0.5)^6$ or $P < 0.05$.

For the other relationships, we had to rely on indirect parameters (Fig. 1), correlated to the winscore. Intake, defined as percentage of the food eaten (Pearson's correlation; $r = 0.53$, $n = 42$, $P < 0.01$), time spent in the food-tray ($r = 0.44$, $n = 42$, $P < 0.01$) and time spend feeding ($r = 0.47$, $n = 42$ $P < 0.01$), were all positively related to the winscore. Birds winning most fights were often found near the food tray and foraging and achieve higher intake. In Fig. 2, we plotted for each individual the dominance rank as a function of its former territory. The dominance position is expressed as the percentage of individuals over which the focal bird was dominant. Note that individuals were only tested against other individuals of the same sex. Dominance rank was not related to former breeding position (Kruskal–Wallis ANOVA $\chi^2 = 0.95$, $n = 10$, $df = 2$, $P = 0.6$). Nor was there a trend that residents were dominating the other categories (i.e. lumping the two leapfrog categories: Kruskal–Wallis ANOVA $\chi^2 = 0.013$, $n = 10$, $df = 1$, $P = 0.9$).

Table 1 Dyads among male and female oystercatchers (*Haematopus ostralegus*). The figures represent the number of interactions won

Winners↓	Losers →					
Males						
	♂1	♂2	♂3	♂4	♂5	♂6
♂1	x	**16**	–	**37**	**23**	**5**
♂2	0	x	**71**	**9**	0	0
♂3	–	0	x	**11**	1	0
♂4	0	0	0	x	**5**	2
♂5	0	0	0	0	x	2
♂6	0	0	0	0	1	x
Females						
	♀1	♀2	♀3	♀4		
♀1	x	**41**	**40**	**10**		
♀2	0	x	**8**	1		
♀3	3	0	x	**26**		
♀4	0	0	0	x		

Figures in bold indicate dyads where the dominance relation could be assigned directly on the basis of agonistic behaviour. For others we had to rely on related parameters. One dyad (♂1 versus ♂3) was not tested

Dominance relations in the field

Winscores collected in the field ($n = 34$), as a function of the territory occupied later in the season (Fig. 3), revealed a difference between residents and leapfrogs. The average winscore was 0.35 and residents won more fights (median winscore 0.40, average 0.45, $n = 16$) compared to leapfrogs (median winscore 0.20, average 0.30, $n = 18$). This trend is significant if we allow one-sided testing (Hierarchical Linear model, Wald $\chi^2 = 0.392$, $df = 1$, $P = 0.0678$ two-sided). The interactions status × sex: (Wald $\chi^2 = 1.294$, $df = 1$, $P = 0.255$), sex (Wald $\chi^2 = 0.977$, $df = 1$, $P = 0.32$) and number of interactions (Wald $\chi^2 = 0.075$, $df = 1$, $P = 0.78$), did not affect the winscore. The observed residents and leapfrogs did not differ in wing length (ANOVA $F = 0.141$, $df = 1{,}30$, $P = 0.710$), tarsus + toe ($F = 0.622$, $df = 1{,}26$, $P = 0.437$), head + bill ($F = 0.030$, $df = 1{,}17$, $P = 0.865$) or bill length ($F = 0.601$, $df = 1{,}30$, $P = 0.444$).

Discussion

Observations in the field were collected in late winter and early spring. In spring and summer, pairs occupy territories (see Methods) and, within the boundaries, they 'win' all interactions, but they may 'lose' interactions outside their territory. Similarly, floaters may win interactions at the social gatherings, or on foraging-territories (only occupied in spring and summer), but

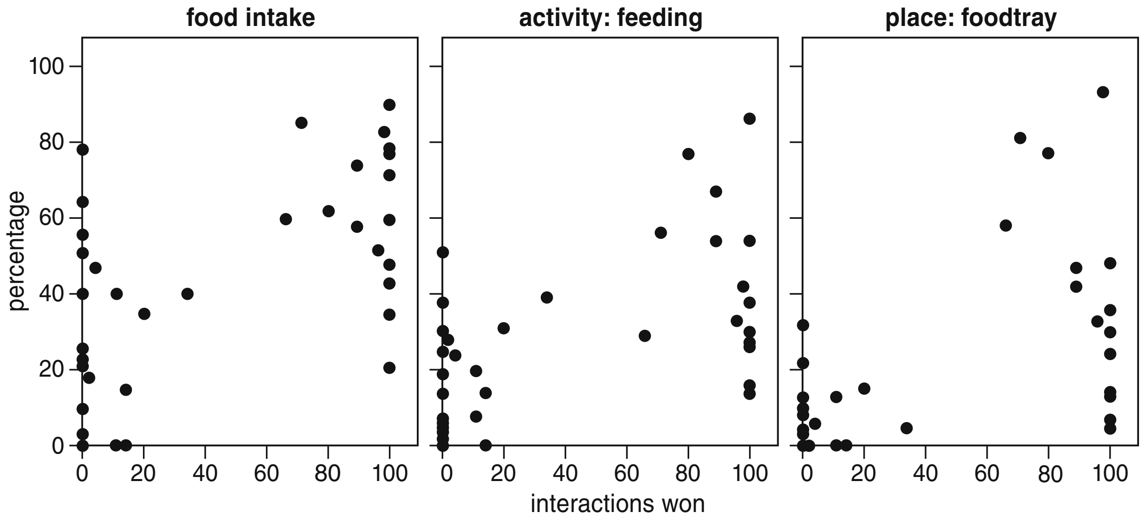

Fig. 1 Behavioural parameters of caged oystercatchers (*Haematopus ostralegus*), which were positively correlated to winscore. Each dot represents an individual bird in a single trial

may lose elsewhere (Heg et al. 2000; Bruinzeel and van de Pol 2004). Within the territorial area, the outcome of an interaction strongly depends on the location where the interaction takes place (Heg et al. 2000), and this site-dependency makes it difficult to compare competitive capacities between individuals in a summer field situation. However, in early spring, when oystercatchers are not yet territorial and foraging occurs in large groups, agonistic interactions over food may be a reflection of their competitive abilities to obtain or defend a breeding site later on. We are convinced that the observed interactions were not related to territory defence for several reasons:

(1) The location where the interactions took place differed from day to day and the locations did not harbour territories of marked individuals in previous years, furthermore locations of territories are nearly identical from year to year (Ens et al. 1992; Heg et al. 2000).
(2) Territory defence is a cooperative enterprise between the sexes and the species has long lasting pair bonds. Only the mate is tolerated within the territory boundaries and in early spring no associations between males and females where observed; in addition birds were at that time foraging in groups.
(3) The majority of fights were 'lost' (the average winscore was 0.35), while in territory disputes nearly all interactions are 'won' (see Bruinzeel and van de Pol 2004).

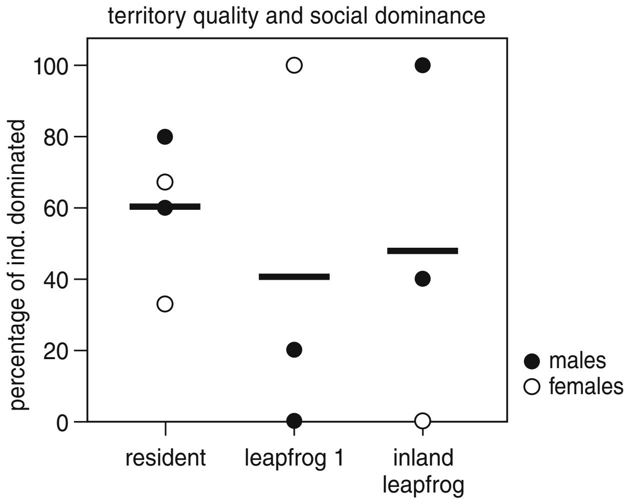

Fig. 2 Dominance rank as a function of former territory for males (*closed symbols*, $n=6$) and females (*open symbols*, $n=4$). The dominance rank is expressed as percentage of individuals over which the focal bird was dominant. The *lines* represent the average per breeding status

Individual quality and territory quality

To understand population regulation it is important to know whether observed differences in reproductive performance between individuals are caused by differences in intrinsic phenotypic qualities between individuals, or by differences in habitat quality by 'equal' individuals. Similarly, density dependent population regulation in heterogeneous habitats may be caused by habitat selection or competition among the breeders (Both 1998). Habitat selection resulting in progressively more low quality habitat to become occupied as density increases, and hence average reproductive success decreases, is a potentially strong regulatory mechanism (Dhondt et al. 1992; Ferrer and Donazar 1996; Rodenhouse et al. 1997). If breeding success of the birds in high quality habitat is unaffected by an increase in density, individuals are distributed 'despotically'. Birds residing in high

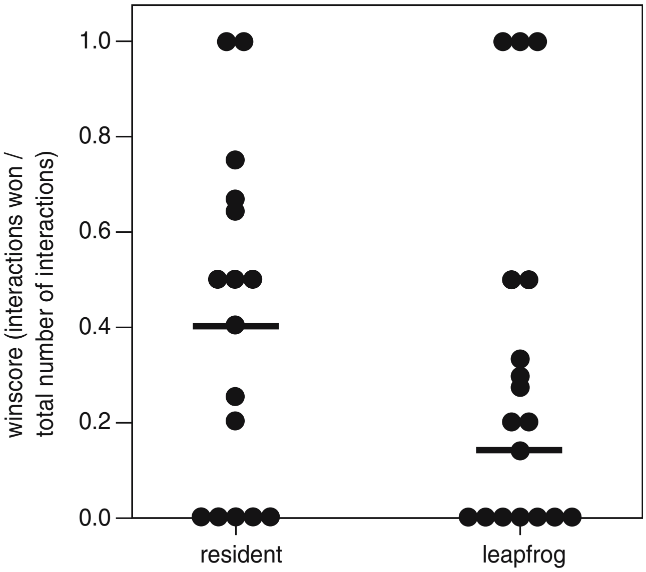

Fig. 3 Winscore (number of interactions won divided by the total number of interactions involved) collected in early spring for individuals later occupying high- (residents) and low-quality territories (leapfrogs). The *lines* represent the median values

quality habitat despotically exclude others, which are destined to reproduce in inferior habitats. At the other extreme, one can imagine that all individuals are similarly affected by an increase in density and this will result in breeders distributed in an 'ideal free' manner. In small passerines, there is evidence for both hypotheses (Dhondt et al. 1992; Both 1998; Przybylo et al. 2001). Experimental density manipulations are rare and often difficult to perform, and results have shown unequivocal effects on for instance clutch size (Both 1998). In pied flycatchers *Ficedula hypoleuca* (Alatalo et al. 1986), older males arrive first on the breeding grounds, and these males are the blackest and seem to be preferred by females. Investigators were able to uncouple the quality of the male from the quality of the territory and females showed a strong preferences for high quality territories and less pronounced preferences for the males occupying those. In willow warblers *Phylloscopus trochilus*, however, females choose for male quality and not for habitat quality (Arvidsson and Neergaard 1991). Considering the timing of breeding, experimental evidence suggests that territory quality is the main explanation for the causal relation between breeding onset and reproductive success (Brinkhof et al. 1993).

Queuing and inferior phenotypes

Ens et al (1995) showed that, in oystercatchers, a despotic distribution can be maintained by a trade-off between age at maturity and habitat quality among new settlers, in combination with a strong prior residence effect (Krebs 1982) for those already settled. Differences in individual quality were not a necessary premise to explain why birds accept inferior sites. In this paper, we have shown that oystercatchers occupying high quality breeding sites more often win a conflict in the field compared to those occupying a low quality breeding site, and that these differences are not related to biometry. In their study, stressing that phenotypic differences are not needed to explain the occupancy of low quality breeding sites, Ens et al. (1995) rejected the inferior phenotype hypothesis on the debated assumption that body dimensions are related to dominance/fighting capacities. For oystercatchers, this correlation seems partially true, but in the opposite direction. Oystercatchers in the Exe estuary (England) with consistent low dominance scores over the years were larger (had longer bills and longer wing lengths) compared to individuals which were in some years dominant (Caldow and Goss-Custard 1996). These authors also showed that dominance can fluctuate over the years, and cannot, therefore, be very strongly linked to adult biometry, which is not that variable over the years. Evidence for the absence or a negative relation between body size and dominance comes from song sparrows *Melospiza melodia* (Arcese and Smith 1985), house finch *Carpodacus mexicanus* (Belthoff et al. 1994), black-capped chickadees *Poecile atricapilla* (Ramsay and Ratcliffe 2003), magpies *Pica pica* (Eden 1987; Komers and Komers 1992), house sparrows *Passer domesticus* (Solberg and Ringsby 1997), brown-headed cowbirds *Molothrus ater* (Teather and Weatherhead 1995) and dippers *Cinclus cinclus* (Bryant and Newton 1996). However, a positive relation between size and dominance was found in harris' sparrow *Zonotrichia querula* (Watt 1986), blue tit *Parus caerulescens* (Braillet et al. 2002), willow tit *Parus montanus* (Hogstad 1987; Koivula et al. 1993; but see Lahti et al. 1996), dark-eyed junco *Junco hyemalis* (Baker and Fox 1978; Jackson 1991), red-winged blackbirds *Agelaius phoenceus* (Searcy 1979), and white-throated sparrows *Zonotrichia albicollis* (Dearborn and Wiley 1993). In great tits *Parus major*, birds in low and high quality habitat were similar sized in the United Kingdom (Riddington and Gosler 1995). However, in Sweden, birds in high quality habitat were larger (Lemel 1989; Ulfstrand et al. 1981).

In our captive trials some individuals (notably the low ranking males: ♂5, ♂6) avoided interactions. In the natural situation, low ranking birds might also avoid congregations of aggressive conspecifics. If that is the case, we might expect that in reality the difference is even larger between residents and leapfrogs. This difference is significant if we allow one-sided testing. Arguments to test a difference between residents and leapfrogs only in one direction are rooted in biological information. Each year, breeding success of residents is 3 times higher than for leapfrogs (Heg 1999; Ens et al. 1992). Recent evidence suggests that the expected lifetime reproductive success of leapfrogs is lower and not in balance compared to that of residents. The age of first reproduction between the two groups is not different (van de Pol et al. 2005) in contrast to model predictions (Ens et al. 1995).

Furthermore, offspring produced by leapfrogs have a much lower chance of recruiting locally and, if they succeed, they can only recruit in low quality habitat, while birds born in high quality territories can recruit in both types of territories (van de Pol et al. 2005). Residents regain a territory faster after a breeding pause compared to leapfrogs (Bruinzeel 2004). Genetical differences have not been found with respect to territory quality (van Treuren et al. 1999). Furthermore, the number of occupied leapfrog territories have dropped, while the number of occupied resident sites have remained constant (Heg et al. 2000), indicating that these are less favoured sites. In our opinion, the combination of these findings warrant one-sided testing. However, more important is the finding that within the residents and the leapfrogs the variance in winscore is very large. On average, there is a statistical difference between the two groups occupying different territories, but this difference has little power to predict the outcome of individual encounters, therefore failing to show this pattern in our captivity trails. Similar findings, where group differences might get obscured by strong individual differences, applies to the age of first reproduction (van de Pol et al. 2005). Clearly, individual variation plays a very important role in this species and future work should concentrate more on explaining variations between individuals occupying territories of similar quality.

Zusammenfassung

Konkurrenzfähigkeit von Austernfischern *(Haematopus ostralegus*) in Territorien unterschiedlicher Qualität

Das Resultat von Habitatheterogenität bei territorialen Arten ist oft, dass sowohl Gebiete hoher als auch niedriger Qualität von verschiedenen Individuen besetzt werden. Erwachsene Tiere die nicht brüten, können Territorien niedriger Qualität akzeptieren, weil sie keine Territorien hoher Qualität erlangen und verteidigen können (‘minderwertiger Phänotypus-Hypothese’), oder weil dies auf lange Sicht eine alternative Strategie zu hochwertigen Territorien bedeutet (‘Warteschlangen-Hypothese’). Territorien von Austernfischern (*H. ostralegus*) unterscheiden sich konsequent in der Anzahl von Nachkömmlingen, die dort jedes Jahr hervorgebracht werden, und dieser Unterschied steht im Verhältnis zum Abstand zwischen Brut- und Nahrungsaufnahmegebiet. Die ‘minderwertiger Phänotypus-Hypothese’ wurde bisher auf Grund fehlender morphologischer Unterschiede (von denen angenommen wurde, dass sie Konkurrenzfähigkeit repräsentierten) zwischen Brutvögeln verworfen. Wir haben das Verhältnis zwischen sozialer Dominanz und Qualität des Brut-Territoriums im Freiland und in Gefangenschaft untersucht. Im Freiland wurden Konflikte öfter von Vögeln mit Territorien hoher Qualität gewonnen als von Vögeln mit Territorien niedriger Qualität; dieser Unterschied wurde jedoch aus dem eingeschränkten Datensatz über in Gefangenschaft lebende Vögel nicht ersichtlich. Diese Ergebnisse werden im Zusammenhang mit der voraussichtlichen Fitness auf lange Sicht bei der Wahl von Territorien hoher und niedriger Qualität diskutiert.

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